XXXII. *Further Remarks on the Organs of the Antennæ of Insects, described in a Paper published in the 'Transactions of the Linnean Society,' vol.* xxii. *p.* 155. *By* J. Braxton Hicks, *Esq., M.D. Lond., F.L.S., &c.*

Read May 5th, 1859.

On the 2nd of June, 1857, I read a paper before this Society, describing some "peculiar structures in the Antennæ of Insects," which was published in the 'Transactions,' vol. xxii. p. 155; since which time I have extended my inquiries among the different tribes, the results of which I have now the pleasure of laying before you. But before doing so, it seems to me that it would be well to give an outline of what had been previously accomplished towards the determination of the structure and uses of the antennæ, and of the various opinions founded upon those researches.

I shall first of all quote Burmeister, who, in his 'Manual of Entomology,' translated by Shuckard, 1836, p. 295, § 195, says, "But as insects doubtlessly hear—as some, for example the Cicada, Grasshopper and May Beetle, &c., produce a peculiar sound, which serves to attract the attention of the female—they must evidently be provided with an organ of hearing, which is either very recondite, or referred to organs whose form does not evince their function. The antennæ are doubtlessly of this class; and, indeed, Sulzer, Scarpa, Schneider, Bockhausen, Reaumur, and Bonsdorff considered them organs of hearing. That they are not organs of touch is proved, anatomically, by their hard, horny upper surface, and physiologically by the observation that they never use them as such, this function being exercised by other organs, viz. the palpi. Besides, the analogy of the Crabs, in which it is well known that the organ of hearing lies at the base of the larger antennæ, speaks in favour of the opinion of their being in general organs of hearing. If after this hint we look to the insertion of the antennæ, we likewise detect here a soft articulating membrane, which lies exposed, and which is rendered tense by the motion of the antennæ. This membrane, beneath which the nerve of the antenna runs, might, without much inconsistency, be explained as the drum of the ear, and thus would the antennæ be transformed helices, which, as very moveable parts, would receive the vibrations of the air caused by sound, and act as conductors to it. Whoever has observed a tranquilly-proceeding Capricorn Beetle which is suddenly surprised by a loud sound, will have seen how immoveably outward it spreads its antennæ, and holds them porrect, as it were with great attention, as long as it listens, and how carelessly the insect proceeds in its course when it conceives that no danger threatens it from the unusual noise. Carus, Straus-Dürckheim, and Oken are of the same opinion, which I have entertained for years, and endeavoured to confirm myself in by numerous experiments."

§ 196. "Much more doubt and uncertainty attend the observations and opinions upon the organ of smell of insects. Reaumur, Lyonet, and several modern French anatomists consider the antennæ as such; but I would ask, with what right? The hard,

horny organ, displaying no nerve upon its surface, cannot possibly be the instrument of smell, for we always find in the olfactory organs a soft, moist mucous membrane furnished with numerous nerves. No such tunic is to be found in insects, at least in their head, or upon the surface of their bodies."

Robineau Desvoidy (see Ray Society vol. for 1845) considers there is still doubt on the the point. "He has already shown, in year 1827, that in the Crabs, as the outer antennæ are evidently the seat of hearing, so the inner ones are the seat of smelling; and afterwards proved, in his 'Recherches sur l'organisation vertébrale des Crustacés, des Arachnides, et des Insectes,' 1828, that in the Isopodes the sense of hearing is no longer doubtful; in the Arachnides it is wanting, while, on the other hand, the parts pointed out as the mandibles are here organs of smelling, and the poison-canal in them corresponds to the lacrymal passage of the higher animals. In the Insects the antennæ are organs of smelling, and usually also of touch. They have no organs of hearing at all."

Küster (see Ray Society vol. for 1847, p. 306) assigns to the feelers (antennæ) of insects the function of smelling. In some experiments with turpentine in glass tubes the reporter says, "If these experiments show that the feelers betray a sensibility to the effect of powerful odours, it is not yet proved that these act on them directly; and so the evidence that the sense of smell has its seat in the feelers is defective."

Newport has given us a valuable paper on the use of the antennæ of insects, in the 'Transactions of the Entomological Society,' vol. ii. p. 229 (read in 1838, but prepared in 1831). He examined the antennæ of *Ichneumon Atropos*; he found all the joints, except the second, perforated all around by very minute holes. This, he says, is the structure of nearly all the setaceous antennæ. He observed two tracheæ passing up its whole length, which gave off branches at every joint, and which seemed to him—but of that he was not quite certain—to communicate with the holes in the antenna-wall. He also noticed a nerve passing throughout its length.

From this, and from analogy with other animals, he judged it probable that the antennæ were not organs of smell. He instituted a series of interesting experiments which led to the same conclusion, and mentions that "*Copris Molossus*," when in motion, extends the plates on the end of its antenna, as if to direct the insect in its course; but that on the occurrence of any loud and sudden sound, it instantly closes the plates and retracts the antennæ, as if injured by the percussion, while the insect stops and assumes the appearance of death. The Geotrupides also behave in like manner. He says, "In conclusion, from all that has been observed of the antennæ, it seems probable that in all insects these are the auditory organs, and that the means by which they are fitted for the function of hearing are varied in different insects, to adapt them to the perception of sounds, according to the habits of the species; that in some species they are endowed also with the sense of touch; that they are of great, although not of vital importance to the insect; and that the loss of both of them, more particularly when endowed also with the sense of touch, will clearly explain in every instance the agitation, delirium, or stupor of the insect, it being in fact tantamount to a total deprivation of the faculty of hearing, feeling, and, I might almost add, of speaking."

The most advanced investigations into the anatomy of the antennæ I had met with, on

the occasion of reading my former paper, were those by E. F. Erichson, published at Berlin in 1847, and contained in his 'Dissertatio de fabricâ et usu antennarum in Insectis,' in which he states that he has arrived at the following laws :—

"1. Antennarum testam in insectis nequaquam solidam, sed numerosis poris perforatam esse.

"2. Poros hosce ab interiore parte membranâ tenui clausos esse.

"3. Poros in variorum insectorum antennis variis modis dispositos esse."

He then proceeds to show the position of these closed pores in the various forms of antennæ, and that they are never found on the basal joints. He describes the dilated third joint in *Musca* as alone possessing these pores, and considers the seta to be the true continuation of the antenna, which view had already been promulgated by Mr. Curtis. He also notices the numerous hairs on the antenna, between the pores, which he considers to form a protection to them from extraneous bodies. Now these pores he regards as organs of smell; because, he remarks, the olfactory organs of the higher animals are moist membranes in order that the odorous particles may be dissolved by the humour secreted, therefore he doubts not that these membranes perform the same office, protected by the downy hairs, and retained moist by them. Another reason for which he considers them organs of smell, is that they are more numerous in those tribes whose scent is acute.

Of this work I was not aware at the time of reading my former paper, it being very scarce. The plates accompanying it simply show holes or pores, closed in by a delicate membrane.

Vogt (Zoologische Briefe, vol. i. p. 516–17, Frankfurt a. M., 1851) says, "If these uniform feelers are examined with a sufficiently high magnifying power, the outer surface of all the divisions, except the articulating joint, is found to be covered with minute punctures, which are closed in at the bottom by a thin membrane that appears to be clothed with numerous hairs. In the antennæ that are not of a uniform shape throughout, there is a shaft or style, and these pores or indentations are then found only upon the toothed processes, branches, and feathers of the feelers, whilst the integument of the shaft is constituted like that of the remaining portions of the body. The peculiar structure of the antennæ is, no doubt, closely connected with their functions; but it would be going far to say, with some recent observers, that it affords undeniable proofs of the correctness of the oft-contested theory that they are organs of smell only." He then says, "We are of opinion that these minute pores, filled with fine hairs, perform a function combining those of smell and touch; for it is an undoubted fact that many insects, such as Ants, Crickets, and others, constantly employ their antennæ to touch and recognize objects, and that nocturnal creatures of this class, especially, possess a remarkably acute sense of touch in the organs; whilst others, again, as the Longicornia, in which these organs are considerably developed in size and form, make no such use of their feelers. On the other hand, we know of no other organs of smell in insects; and all attempts to find the seat of this sense have been hitherto ineffectual."

Thus we see how many different opinions have been entertained regarding the functions of the antennæ. Sulzer, Scarpa, Schneider, Bockhausen, Reaumur, Bonsdorff, Carus, Straus-Dürckheim, Oken, Burmeister, Kirby and Spence, and Newport are all in favour

of their being auditory organs; whilst, on the other hand, we have Lyonet, Robineau-Desvoidy, Küster, Erichson, and Vogt in favour of their being olfactory organs. In point of number, the majority are evidently in favour of their being organs of hearing, though it appears to me that some on either side base their opinions on but slender foundations, and that the most important advocate on the olfactory side, Erichson, has formed his opinion upon an imperfect knowledge of the true nature of the organs: he has thought them to be closed perforations opening internally; whilst I have, in the paper mentioned, shown them to be closed sacs, sometimes considerably convoluted, to the inner aspect of which the nerve passes. I shall, in the course of the present paper, show that by no means in all cases is the closing-in membrane thin and delicate, but that in some insects it is thickened and even raised into a conical and hair-like eminence; his arguments, therefore, regarding its analogy to the pituary membrane clearly cannot hold. None of these writers, and, so far as I am aware, no one else, had at the time when my former paper appeared pointed out these closed, chambered sacs; and it is evident that the opinions concerning the functions of the antennæ, hitherto entertained upon an imperfect knowledge of their structure, will undergo considerable modification when the structures I have already, and those which I am now about to describe, are duly considered and re-investigated.

I shall now proceed to the detailed description of the other antennæ which I have examined since my last paper. At that time I had not investigated the antennæ of the Coleoptera to any extent; but I find they form no exception to the rest of the Insecta.

1st. In *Necrophora Vespillo* the organs are only found on the last three joints, two of which are foliaceous, while the terminal one is rounder and pointed at the apex, forming the club or clava; and a fourth, foliaceous joint does not possess these organs.

The sacs are found on both sides of the leafy joints, and all round the terminal one, though they are larger on the back. At A. fig. 1 (Pl. LXVII.), I have shown the surface enlarged, with the covering-in membranes and position of the hairs between them. At A. fig. 2. is the section of the same. The average diameter of the sacs is about $\frac{1}{3500}$ inch.

The distribution of the nerve, spreading by many branches throughout the breadth of the joint, can be seen by focusing for the centre of the lamella. This antenna is mentioned by Erichson, who, after describing its form, says of the last three joints, "Testa ei est poris subtilissimis creberrimisque perforata, relictis nonnullis areis minutis impressisque, e quibus setula nascitur" (*op. cit.* § 10). It is these pores I have drawn at A. fig. 2, showing a sac which can be clearly made out in the bleached antenna.

In the genus *Silpha* there are eleven joints: the last three are dilated and covered with fine hairs; and scattered equally over the surface is to be found a number of sacs, one-fifth less in quantity than the hairs, B. fig. 1 *b b*. Besides these, there are larger sacs, B. fig. 1 *a a*, principally found on the terminal joint, about twenty-four in number. These show clearly the form of the organs from above, and at B. fig. 2 their nature can be further understood in section. The covering-in membrane is delicate, and rises as a low cone from the general surface-level; between the organs the hairs arise and overhang them. The diameter of the larger ones at the surface is $\frac{1}{1760}$ inch. This is the character of the antenna throughout all the genus, so far as I have ascertained.

In *Creophilus*, and probably in kindred genera, the organs are found only on the

terminal joint, which is more elongated than the rest: they consist of the smaller and larger sort, as in *Silpha*, but arranged in a manner very peculiar, and confined to the lower half of the terminal joint. The smaller forms are disposed in groups of from six to sixteen in each. The groups are diamond-shaped, with a row of hairs between them: at the angle are occasionally found the larger organs, as in *Silpha*, as also a few scattered on the upper half of the joint. Their covering-in membrane, however, is not so conical. The diameter of each of the small organs is $\frac{1}{5400}$ inch. (See C. fig. 1.)

In *Goerius olens* the organs are distributed thickly over the surface, rather more frequently than the hairs, and show their sacculated nature very well (D. *a a*).

In *Carabus* there are eleven joints in the antenna; only the last five possess the organs. They are not so numerous as those I have described before, and are principally placed on one side of the antenna, as shown in E.

In all the species examined of this genus, I have found the closing-in membrane raised considerably above the surface-level, more so than in *Silpha*, and having six or eight ridges running from apex to base, as is shown in E. figs. 2, 3. The greatest diameter of the sac is $\frac{1}{1660}$ inch, while that of the closing-in membrane at the surface is $\frac{1}{3000}$ inch. The Section, fig. 1, shows the form of the sacs and closing-in membrane.

In six species of *Elater* which I have examined, I find the same conditions, namely: chiefly on the serræ of the joints, generally in front of the base of the hairs, are small sacs about $\frac{1}{3000}$ inch in diameter, as is shown in F. figs. 1, 2 *a* & *b*. The closing-in membrane is slightly raised above the surface; and on the apex are from three to six, generally four, small papillæ or tubercles, as is shown in F. fig. 2 *b*, & fig. 3.

In *Strangelia elongata* these sacs are very numerous, disposed over eight of the twelve joints, and becoming larger and more frequent towards the apex. They are generally situated in front, or near the roots of the hairs; and their closing-in membrane is much smaller than the diameter of the sacs beneath. These sacs vary much in size, being from $\frac{1}{3750}$ to $\frac{1}{6000}$ inch in diameter. The larger sort seem convoluted, or two- or three-chambered.

The antennæ of the Musk Beetle (*Aromia moschata*) are very similar; and the same description will apply, except that the sacs are larger than the above.

In *Cetonia aurata* the three lamellæ are furnished with sacs, which are placed close together, and are found on both sides of the middle one only, and on that side of the first and third which is in contact with the middle one.

In the antenna of *Dynastes Hercules* the sacs are very numerous, and the covering-in membrane well marked, their diameter being about $\frac{1}{3700}$ inch. They are found on the same parts of the lamellæ as in *Cetonia aurata*. In consequence of the sacs not extending through the whole thickness of the antenna-wall, a tube passes from the inner aspect of each to connect it with the interior of the lamella: towards the margin of the lamella the form is modified, the sac being placed halfway within the thickness of the integument; and there is not only a tube connecting it with the interior, but also a smaller one extending to the outer surface (H. figs. 1, 2). Numerous depressions, in some cases forming cavities, are to be found in the antenna; and in all the Lamellicorns I have hitherto examined, the sacs are situated on all portions of these depressions, which are thus common to them.

In some of the Lamellicorns the closing-in membrane is prolonged to a point, sometimes rigid, so as to be easily mistaken for a hair; but closer inspection and comparison, I am sure, will satisfy any one as to its true nature. I can best explain what I mean, by the antenna of *Geotrupes stercorarius*. The surface of the lamellæ is patterned all over in the same parts as in the former Lamellicorns, and in a very similar manner to those of *Andrena fulva*, shown in fig. 8 of my former paper. The surface is occupied with about an equal number of true hairs, and articulated projections very like hairs (I. fig. 2 *b*), beneath each of which is a sac, as in the former kind of antennæ; and as the sac does not extend through the whole thickness of the antenna-wall, there is, as in *Dynastes*, a tubular communication with the interior of the lamella. (See I. figs. 1, 2.)

This structure will help to explain other forms in the Lamellicorn groups, as for instance in the Stag Beetle (*Lucanus Cervus*). Over the same parts as in the others are a number of apparent hairs, slightly curved, projecting from the antenna-wall. On looking more closely, it will be observed that they are not all true hairs; on the contrary, only a few of the larger ones are hairs, while beneath the rest an elongated sac is placed, as is shown at K. figs. 1, 2. In this insect the terminal lamella has a large cavity—sometimes there are two—extending deeply into its interior (fig. 3). The diameter of the sac is $\frac{1}{2100}$ inch.

A similar condition exists in *Hydrophilus piceus*; but the nature of the sacs is well shown by the fact that some have the closing-in membrane level, and others slightly raised, whilst some have it prolonged into a spine (G. fig. 2). The diameters range from $\frac{1}{1660}$ to $\frac{1}{3700}$ inch. This peculiar-shaped antenna has nine joints; the last three are liberally furnished with these sacs, and of a larger size than any I have hitherto found: possibly the size of the insect will account for it, though it may generally be said that the size of the insect has but slight relation to the size of the sacs, as will be seen by comparing the various measurements I have given.

That these sacs with hair-like apices are the same as those which are found in *Melolontha*, *Dynastes*, &c. is evident from the facts—1st, that they are situated in the same position; 2nd, that some have level, others spinous apices on the same antenna; 3rd, so far as I have found on examination of a large number of insects, I think it may be laid down as a rule, that no cuticular projection or spine has a cavity or sac beneath it in any other part of the insect, except in the antennæ. In some *Hemiptera* I have found beneath the true hairs a cavity, but not like these sacs, inasmuch as the whole antenna-wall was protruded, with a true hair at the apex.

The spinous condition of the covering-in membrane is an important point, because it seems to be clearly at variance with what is generally understood to be the structure of an olfactory organ. Again, when we consider the habit of *Hydrophilus* and compare it with another aquatic Beetle, *Dyticus marginalis* (to be presently alluded to), I think we may obtain a clue as to the nature of these organs in the antennæ. If watched attentively, it will be seen that the *Hydrophilus* is very careful not to wet his antennæ. The moment he is placed in water he suddenly brings them beneath the joint of the head and thorax, where they remain in a hollow, surrounded by the silvery film of air which covers the under surface of the thorax, and which is collected by the numerous downy hairs on

that part of the body. If this insect employed its antennæ to scent its food, which is aquatic, does it not seem very improbable that the olfactory organs should be carefully shut off by a peculiar provision, from the medium in which both the insect and the food are, and which medium is known to be well fitted for the diffusion of odorous particles? Now in *Dyticus marginalis* we shall see the reason that its antennæ are bathed with the water,—not because it uses its antennal organs for scent, but because it uses them as instruments of touch, and has them provided with special organs for that purpose.

The antenna of *Dyticus marginalis* (L.), very similar in general appearance to the palpi of *Hydrophilus piceus*, consists of nine joints, all nearly alike, except the terminal one, which is pointed. The antenna is almost universally smooth: the only representatives of the hairs are on the prominent parts of the joints and apex, which I will describe shortly. But on one side of the upper part of each of the joints are a number of circular depressions (L. fig. 1 *b b b*, fig. 3.), of the diameter of $\frac{1}{3000}$ inch, more numerous towards the apex of the antenna; in the centre of each circular depression is a short canal, which enters a sac having its interior aspect in communication with the interior of the antenna; whether closed or not it is difficult to determine, but it appears to be so by a firm substance frequently found on the inner surface of the antenna where these organs are present. The nerve is to be seen very plainly giving off branches as it passes up the antenna to each of these groups, and finally expends itself in those of the apex, sending off a branch to the roots of the hairs.

To these hairs, of which I have given a drawing (L. figs. 2, 4), I would also request attention, because of their peculiar form, and because such a form is not uncommon in insects, both on the antennæ and palpi, when those parts are used as organs of touch. That all the hairs, long as well as short, possess to some extent the faculty called in the higher animals "general feeling," I think cannot be doubted for a moment; but hairs of the form I am about to describe seem, from their position and shape, to be specially adapted as instruments of that more refined tactile sense called "touch." Perhaps the most marked example is to be found in the antenna of *Dyticus marginalis*. The organ in question consists of a widened follicle (L. fig. 1 *a a a a*, figs. 2, 4), becoming gradually narrowed to the centre, from which a delicate membrane, in the form of a depressed cone, stretches across; from the centre of this membrane springs the modified hair, something like a ninepin, its apex reaching a little above the general surface of the antenna. There are three on the apex of the antenna, three on each side of the widest part, and two or three on each side of the upper end of each joint at its widest part. Their situation on the prominent parts will show their use for touch; and the habits of the insect also show how valuable as a tactile organ is its antenna.

The whole of the antenna of this insect is wetted by the water, in which it passes the greater part of its life, and where it finds its sustenance. In form the organs on them are not essentially different from those before described in other insects; but it is difficult to suppose that odorous particles could pass through a membrane, then through a very small tube into a sac, itself probably closed, before they could affect the nerve placed at the inner surface; while it is easy to understand how such a structure is well adapted for hearing in water. In the larval antennæ no such organs are found: the hairs on them

are few and long; whilst the apex, which has three spinous processes which are supplied with a nerve, doubtless possesses the sensation of touch (see M. figs. 1, 2, 3).

In *Meloe* the antennæ consist of eleven joints, of which the 1st, 2nd, 3rd, and 9th are not furnished with the organs, as all the rest are, especially the 6th, 7th, 10th and 11th: those in the last, or 11th, are the largest. They have the same form as those of the *Necrophora Vespillo*, but rather smaller.

In *Clytus arcuatus* the sacs are found interspersed between the hairs, of the diameter of $\frac{1}{3000}$ inch, in considerable number on the last five joints, and of the same form as in *Necrophora Vespillo*.

I shall next describe the antennæ of the *Hymenoptera*.

In the genus *Vespa*, whose antenna I have described in my former paper, I have since had an opportunity of examining the antenna of the male, female, and neuter, both of *V. vulgaris* and also *V. Crabro*. In all these, as there described, the last ten joints are covered on all sides from base to apex by organs having the canoe-shaped closing-in membrane. The number of these on each antenna of *V. vulgaris* is prodigious; on each segment there are rather more than 2000. The 3rd segment possesses rather fewer, and the 12th rather more, making altogether on the ten segments 20,000 for each antenna. There are also on this antenna many dwarfed hairs, as on that of *Dylicus marginalis*. There is no particular difference between the different sexes and neuters; and I may add that a distinct sac is visible behind the oval opening, which is seen behind the canoe-shaped closing-in membrane.

In *Apis mellifica*, however, the antenna of the worker or neuter (described in my former paper) possesses the organs only on one side; whilst in the drone or male the antenna is entirely covered with them, similar to those of the male *Eucerus longicornis* (see former paper, Pl. 30. fig. 7). I have, unfortunately, not succeeded in obtaining a female or queen, to enable me to institute a comparison: still one would argue that if these organs were olfactory, we ought to find them in a peculiar degree developed in the worker, and scanty in the male, who seldom leaves the hive, and then only for a short distance; but the contrary is the case.

Odynerus murarius possesses organs very like those of the neuter *Apis mellifica*, situated on one side; and as the other side is free from any markings, the nerve and its distribution and the accompanying tracheæ can be beautifully seen. The nerve, accompanied by two tracheæ, passes from base to apex, through the centre, giving off a branch from either side, about the centre of each segment, which branch passes through the next joint, to be distributed to the organs in the succeeding segment, and again giving off numerous fibres to supply the organs with sensation.

A remarkable antenna among the Hymenoptera is that of the Red Ant, *Myrmica rubra*. It consists of twelve segments: the first is very elongated, the rest being joined to it at a right angle; the segments after the second gradually increase in width to the last, which is longer than any, except the first, and tapers gradually to a point, towards which the antenna-wall gradually becomes thinner, so that at the extreme apex it is very delicate, and the hairs also abbreviated. The surface is furnished tolerably thick with hairs, as in most antennæ. It also possesses the sacs very well marked, as may be seen at N. fig. 1 *a*, 3 *a*, 4.

They exist on the last nine segments more towards the distal end of each. The different forms are shown at N. fig. 3 *a a*, fig. 4. : the diameter of the closing-in membrane is about $\frac{1}{2700}$ inch ; the length of the sac is from $\frac{1}{1900}$ to $\frac{1}{1700}$ inch.

But, besides, there is another form of what seems to be the same structure, and which has a rather less-marked parallel in the antenna of *Pronœus inetabilis* (to be described next). There will be observed at N. fig. 1 *b b b*, a number of small closing-in membranes, of a diameter of $\frac{1}{4000}$ inch ; behind each is a very small sac, leading to a long delicate tube, which, bending towards the base, dilates into an elongated sac having its end inverted, as may be also seen in the larger sacs (see N. figs. 2 & 3 *b*). What their specific use may be, it is at present impossible to say ; but, supposing these organs to be auditory, we may easily conjecture that they would be able to appreciate notes in a higher key. The nerve in this antenna is well seen, throwing off branches to the organs in its course upwards.

The antenna of *Pronœus inetabilis* consists of thirteen segments, and possesses three, if not four forms of these organs, disposed in groups on one side of each segment :—

First. In the middle of the segment are a number of small closing-in membranes, of the diameter of $\frac{1}{4300}$ inch ; they are raised above the level of the surface, and have a small elongated cavity behind them, which is shown at O. fig. 1 *d d*, fig. 3 *d*.

Secondly. On the side are level, circular or slightly oval closing-in membranes, with an oval opening just beneath, leading into sacs ; in the centre of each inner surface is a papilla pointing inwards. These are shown at O. fig. 1 *b b*, fig. 3 *b*. The diameter is $\frac{1}{2300}$ inch.

Thirdly. There is a scanty group of organs towards the middle of the segment, whose closing-in membrane is also level and quite circular ; and beneath it is a shallow cavity, having a small opening in the centre leading into a tube, which soon dilates, and is connected with a curved tube, which expands in the form of a trumpet. The exact method by which these trumpet-shaped expansions end internally is difficult to decide, owing to the delicacy of the parts and the thickness of the antenna-wall. It is impossible to make out the exact nature of the junction at the curve. This form I have shown at O. fig. 1 *c c*, fig. 3 *c c*. There is a strong resemblance between these and the long expanding tubules in *Myrmica* ; and they probably have the same function.

Fourthly. On the remaining portion of the half-antennal surface occupied by these structures, are a number of low projections, at first sight like dwarf hairs ; but on closer inspection they will be found to be conical projections of a delicate membrane protruded from the centre of a depression of the cuticle, and having a sac behind : to these the nerve can be plainly seen passing, as in the other forms ; and a quantity of firm granular matter may be observed at the junction of the nerve with the sacs. There is no real analogy between these organs and true hairs. Their diameter is $\frac{1}{1900}$ inch, and they are shown at O. fig. 1 *a a*, fig. 2.

That these different forms are capable of imparting to the insect the power of appreciating notes of different pitch, will scarcely be denied, if we admit that they are auditory organs ; while, if considered as olfactory, it would be difficult to explain the reason of such a variety of forms.

Sirex gigas possesses two forms of these organs, as is shown at P. They are found freely scattered over the segments on one side, the other being free from them. They consist of—

1st. A number of depressions, diameter $\frac{1}{900}$ inch, in the centre of which is a closing-in membrane; beneath is a tube passing through the antenna-wall, and leading to a membrane-sac, as is shown at fig. 1 *b*, fig. 2, fig. 3 *b*.

2nd. A number of closing-in membranes, having a distinct cavity behind them, in the antenna-wall. They are shown in section at fig. 4, and from above at fig. 3 *a*. Diameter at surface $\frac{1}{3000}$ inch. These appear to be nearly the same as at O. fig. 2, and similar to those in *Carabus*.

We come now to the Lepidoptera. In the Diurna I have examined

Gonepteryx rhamni,
Pieris, or *Pontia brassicæ*,
Pontia rapæ,
Vanessa urticæ,
Hipparchia Janeira,
Lycæna Phleas;

and I find the same description will apply to them as to the antenna of *Argynnis Paphia* (of which I have given a description and figure in the paper before referred to), with the exception of a variation in the comparative number of organs, and of the number of cavities.

In the Moths I have as yet only found the smaller organs described in *Argynnis Paphia*: their position on the pectinated forms in the *Bombicidæ* and *Geometridæ* seems to be universally towards the apex of the division; and in the forms less deeply pectinated they are found on those sides where the deepest indentation exists. They are more numerous towards the apex of the antennæ.

I have figured those of *Arctia Caja* (Great Tiger Moth) at Q., showing their position in the male at fig. 1, and in the female at fig. 2. At fig. 3 the same is magnified, showing in the dotted lines the existence of a cavity in the interior.

Q. shows them on the dilated end of the combs in *Odonestes potatoria* (Drinker Moth): fig. 5 shows one enlarged.

This condition I have found to exist in

Drinker Moth (*Odonestes potatoria*),
Yellow-tailed Moth (*Porthesia chrysorrhœa*),
Vapourer (*Orgyria antiqua*),
Lackey (*Clissocampa neustra*),
Ermine (*Pitosoma lubricipeda*),
Willow Beauty (*Alcis rhomboidaria*).

In those antennæ which are simple and filiform, I find that they exist on one side only, and situated towards the distal end of each segment, as in the Buff Tip (*Pygæra bucephala*), and Yellow Underwing Moth (*Tryphæna Bomba*). The latter I have figured at R.: fig. 1 shows their position; fig. 3 shows a magnified view of them, with the peculiar markings on the cuticle, while at fig. 2 the nerve (*a*) is shown distributing branches to

them. In the interior of the antennæ, underlying the organs, is found a lobulated membranaceous mass (fig. 2 *b*), in which the extremities of the nerve lose themselves. It is difficult to make out the precise structure of the mass; but it seems composed of a number of membranous sacculi. It occurs in a great number of insects, and principally, if not always, in those whose organs are not dilated into a distinct sac in the antenna-wall.

In *Pygæra bucephala* I have noticed a depression on each segment of the antenna, similar to those observed in some Coleoptera.

In the Ghost Moth (*Hepialus humuli*) the organs are in appearance more like those of the simple sort in the Diptera, and are dispersed over the whole antenna. The male and female antennæ and antennal organs are precisely alike; and it may be stated, as a rule, that those Moths which possess such an exquisite sense of smell as *Orgyria antiqua* have the organs more developed in the male than in the female, but they do not seem to be more numerous than in those Moths which are reputed to possess a more obtuse olfactory power.

In *Anthocera loti* (Burnet Moth) the organs may be easily detected, being very distinctly placed in a slight depression between the cuticular projections covering that part of the antenna in which they are situated. The closing-in membrane is irregularly circular, of a diameter of $\frac{1}{2300}$ inch, and has a small papilla in its centre (S. fig. 1 *b*, fig. 2 *b*). Behind this is a bowl-shaped sac, which has projecting into it a small papilla in the centre of its inner wall, probably where the nerve impinges. This is shown in the section at S. fig. 2 *a*, while at *c* the hair-like cuticular projections are seen partly overhanging it.

The antenna of *Macroglossa stellatorum* is peculiar in having one side of each segment furnished with numerous rows of hairs. In the centre of each facet may be seen sacs (fig. 19 *a*). These hairs give a peculiar appearance to the antenna. They gradually enlarge towards the exterior of each facet, and possess large roots or follicles.

In *Sphinx ligustri* (Privet Hawkmoth), the organs are to be found from base to apex on every segment, on one side only, and in considerable profusion; and, so far as I can make out, are on the same plan as in the Burnet Moth.

I have examined many specimens of foreign species of *Tetrix* of all sizes, and find the organs are on precisely the same plan, and as numerous, as in the *Tetrix* described in my former paper.

At U, I have drawn the antenna of *Forficula auricularis* (common Earwig). Fourteen segments are found to possess the sacs; from one to three on each, at the distal or outer end, as in fig. 1 *a a a*. Their shape may be seen in section at fig. 2 *a*; their diameter at the surface is about $\frac{1}{2300}$ inch.

I have also examined the antennæ of an *Agrion*: they possess a few (about three or four) of the simple cells I mentioned as occurring in such a clear manner in *Libellula*, while in the common May-fly (*Ephemera diurna*) they exist in but a very rudimentary condition.

In the parasites also, the antennæ are furnished with similar organs, as shown at V.,

where the antennæ of the *Pediculus* of the Crow are represented. Two organs are found on each joint, except the last two. In the *Pediculus* of the Dog the organs are very large; they are shown in profile at V. fig. 1 *b*.

Pulex also has them on each joint, as seen at V. fig. 2. An enlarged view of those of the *Pulex* of the Mouse is shown in fig. 3.

Having now detailed all the principal facts I have been able to secure since my last paper, I shall again endeavour to point out the great advantage to be derived from the process of bleaching which I described at that time, without which it would have been impossible, by reason of the depth of colour of the insect-integument, to have made such advances upon our previous knowledge. It is for this reason that I have no doubt the opinions of the naturalists I mentioned at the beginning of this communication would have been different, had they known the precise nature of the organs behind the closed pores; for it does seem to me impossible that the essential nature of an olfactory organ should be included in the structures just mentioned, and that odorous particles could pass, first through a membrane, sometimes even spinous, then through a cavity filled with fluid, and thirdly through another membrane to reach the extremity of a nerve. On the other hand, it is not difficult to conceive that such a structure would be well suited to the transmission of sound, upon the principles pointed out by Müller; and the numerous modifications of these antennal organs especially to be found in the Hymenoptera, seem to form an additional reason for supposing them to be auditory—namely, that they may give the insects a power of appreciating sounds of various pitch.

Amongst entomologists, some misconception as to the nature of the antennæ has arisen from their not duly considering, in their observations on the habits of insects, that the antenna has (whatever other function it possesses), in a great number of insects, a faculty of feeling superadded, at least in those insects whose antennæ are tolerably mobile. There can be no doubt that most of the Hymenoptera use them as tactile organs; and I am sure that the Honey-bee, *Andrena*, and the *Ichneumonidæ* do so continually, though most writers have considered that the numerous movements of the antennæ of the Ichneumons are for the purpose of smelling; but I am confident that strict observation would confirm my opinion that these motions are for feeling—and thus to enable the Insects to detect the opening of the holes in which the larvæ they are seeking reside; and that the antenna could be used as well for hearing any noise the larvæ made, as for smelling out their position. The Ant has been quoted as an instance strongly showing that the antennæ are used for smelling, as is manifested in the power of mutual recognition possessed by these Insects. Last summer I had opportunities of observing the Wood-ant; and found that it invariably acted in the following manner when two individuals met one another from opposite directions:—First, they approached and brought their antennæ into contact for a moment; then, approaching nearer, they brought their palpi together, and retained them in contact during the whole time, whilst the antennæ never touched each other again. By what means they communicated their thoughts it is impossible to say; but I suspect the palpi played the most important part.

From the various remarks made in this paper, as well as from the observations of

Newport on the habits of insects, I think it may be concluded that the antennal organs are formed upon a plan in accordance with our present ideas of an auditory apparatus, and are therefore capable of hearing, and that:—1st, they consist of a cell, sac, or cavity filled with fluid, closed in from the air by a membrane analogous to that which closes the foramen ovale in the higher animals; 2nd, that this membrane is for the most part thin and delicate, but often projects above the surface, in either a hemispherical, conical, or canoe-shaped, or even hair-like form, or variously marked; 3rdly, that the antennal nerve gives off branches which come in contact with the inner wall of the sacs; but whether the nerve enters, or, as is most probable, ends in the small internally projecting papilla which I have shown to exist in many of these sacs, it is very difficult to say. The principal part of the nerve proceeds to these organs, the remaining portion passing to the muscles, and to the roots of the hairs, at least to those of the larger sort. The distribution of the nerve can be very beautifully seen in the antennæ of the *Pronœus* before mentioned, as also in *Odynerus*.

Another point, which might be mentioned as rather tending by inference to the confirmation of this opinion respecting the antennal organs, is that in the Shrimp and Crawfish among the Crustaceans (which have a sac at the base of the antenna, commonly regarded as the auditory organ) there is no trace of any organs similar to those of the Insecta; the nerve simply supplies the hairs and muscles.

More than a year after the reading of my former paper on this subject, one was read on August 30, 1858, by M. Lespés, before the Academy of Sciences, Paris, reported upon satisfactorily by a Committee, and subsequently published in the 'Annales des Sciences Naturelles:' Paris, 1858. The title of this paper was "The Auditory Apparatus of Insects." Both the author and the reporters seem ignorant of what I had already done on this subject, as, by not being aware of the value of bleaching the integument, M. Lespés had very great difficulties to contend with, which would have been avoided had he used that process, and moreover he would have escaped a great error. He had in consequence to employ the most colourless species; and the most minute of his researches were upon the antenna of the Lamellicorns, *Melolontha*, *Polyphyllus*, &c., and he was obliged to view the organs perpendicularly only. He certainly asserts the existence of sacs behind the membranes, which he calls "*tympanules*," and gives a drawing and description of the ultimate branches of the antennal nerve proceeding to them. But he states that the sac or cell (which he terms "*cellule*," or "*poche*") contains a rounded, transparent, solid body attached to the inside of the membrane; this body he calls an "*otolithe*." Now, in all the numerous antennæ which I have observed with good and high powers, I have never seen this otolithe, the nearest approach to that body being the small chain of solid granules passing, in *Tetrix*, from the centre of the closing-in membrane to the back of the sac. But by following his directions for the observation of these structures in *Melolontha*, by splitting open one lamella of the antenna and viewing the wall from within, I have seen the very same appearance he describes, when viewing it with low powers. However, the apparent otolithe is very soon resolved into its true nature: for by using an $\frac{1}{8}$-inch objective and high eye-piece, the appearance supposed to be the otolithe is seen long before the rest of the sac; and by adjusting the focus, the otolithe

melts away; so that by the time the sac is in the proper focus, the appearance of the otolithe has vanished; and on further examination it will be plainly seen, especially where the sac is viewed obliquely, that the appearance of a solid body was an optical deception, produced by the looking perpendicularly at the tube which passes from the sac behind the tympanum to communicate with the interior of the antenna: as the tube is seldom in the centre, the appearance of the "otolithe" is usually more or less on one side. Another great proof against the existence of an otolithe is the fact, that when looked at sideways the sac is, so far as I can see, perfectly empty.

M. Lespés, with myself, considers these organs to be none other than auditory; and from the numerous researches which have now been instituted by Erichson, Lespés, and myself, I think we may safely say that their existence is very general if not universal throughout the insect tribes.

M. Lespés has also pointed out the peculiar hairs which I had noticed some time since, and which I have figured in the Plate as they exist on the antenna of *Dyticus marginalis*.

Note.—The bleaching process which I now adopt is a slight modification of that formerly recommended. I take chlorate of potash, say one drachm; water one drachm and a half; mix these in a small bottle with a wide mouth, holding about an ounce; wait five minutes, and then add about $1\frac{1}{2}$ drachm of strong hydrochloric acid: chlorine is thus slowly developed; and the mixture remains in action from one to two weeks.

EXPLANATION OF THE PLATE.

Tab. LXVII.

A. *Organs on the antenna of* Microphora Vespillo.

Fig. 1. Enlarged view of the organs, between the hairs. Diameter $\frac{1}{3300}$ of an inch.
Fig. 2. Section of antenna wall, showing the sacs behind the membrane.

B. *Organs on the antenna of* Silpha —— ?.

Fig. 1. Enlarged view of organs, as seen from above, on the terminal joint: *a a*. large sort; *b b*. smaller organs.
Fig. 2. Section of larger organs. Diameter at surface $\frac{1}{1760}$ of an inch.

C. *Organs on the terminal joint of a* Creophilus.

Fig. 1. Shows the lozenge-shaped groups.
a a. Organs from 6 to 16 in each group, divided by rows of hairs. Diameter $\frac{1}{3400}$ of an inch.
b b. Large organs.

D. *Organs on antenna of* Goerius olens.

a a a a. Organs rather more frequent about the hairs.
b b. Hairs.

E. *Organs of* Carabus.

Fig. 1. *C. violaceus*. Section of antenna-wall, showing true hairs, *a a*.
b b. Sacs with covering-in membranes raised above the general level.
Fig. 2. Enlarged view of section of antenna-wall, showing the peculiar markings of the covering-in membranes. Greatest diameter of the sacs $\frac{1}{1600}$. Diameter at surface $\frac{1}{3000}$th of an inch.
Fig. 3. *C. arvensis*. The covering-in membrane seen from above, ribbed more than in *C. violaceus*.

F. *Segment of the antenna of* Elater.

Fig. 1. Shows the sacs generally in front of the hairs.
Fig. 2. Enlarged view of portion of same; *b*. still more magnified, showing four or five papillæ on each.
Fig. 3. Section of the antenna-wall: *a a*. organs; *b*. true hairs.

G. *Organs of antenna of* Hydrophilus piceus.

Fig. 1. Enlarged view of a portion of surface.
Fig. 2. Section of antenna-wall, showing the various conditions of the covering-in membrane.

H. *Portion of antenna of* Dynastes Hercules.

Fig. 1. Part of one lamella. *a a*. Normal sacs.
b b. Sacs distorted at margin.
Fig. 2. Section of antenna-wall. Diameter $\frac{1}{1700}$ of an inch.

I. *Antenna of* Geotrupes stercorarius.

Fig. 1. Enlarged view of upper surface of lamella.
a a. True hairs.
b b. Organs.
Fig. 2. Section of antenna-wall.
a a. True hairs.
b b. Organs.

K. *Antenna of* Lucanus Cervus.

Fig. 1. Surface of lamella, showing the organs and their spines.
Fig. 2. Section of antenna-wall.
a. True hair-follicles.
b b. Organs with spinous terminations.
Fig. 3. Terminal lamella with cavity. There are sometimes two.

L. *Antenna of* Dyticus marginalis.

Fig. 1. Last two segments of antenna, showing—
a a a a. Dwarf hairs (tactile).
b b b b. Peculiar structure on one aspect only (see Fig. 3).
c. Nerve passing to the structures and dwarf hairs.
Fig. 2. Enlarged view of both tactile hairs and organs.
Fig. 3. Enlarged view of organs. Diameter $\frac{1}{3000}$ of an inch.
Fig. 4. Enlarged view of tactile hairs.

M. *Antenna of larva of* Colymbetes striatus.

Fig. 1. Terminal joints.
a. Spine or hair.
b. Apex with three hairs.
Fig. 2. Enlarged view of *b* (fig. 1), showing the nerve.
Fig. 3. Enlarged view of *a* (fig. 1).

N. *Antenna of* Myrmica rubra.

Fig. 1. The terminal and next segment, showing—
a a a a. Organs as in other insects;
b b b. Smaller, communicating with the tubes, as in fig. 2.
Fig. 2. Shows the elongated tubes with expanded extremities, proceeding from *b b b* (fig. 1).
Fig. 3. Section of antenna-wall.
a a. The larger and more usual form. Diameter $\frac{1}{2700}$ of an inch; length from $\frac{1}{1900}$ to $\frac{1}{1700}$ o an inch.
b b. Diameter $\frac{1}{4000}$ of an inch.
Fig. 4. Another form of *a a* (fig. 3).

O. *Antenna of* Pronœus inetabilis.

Fig. 1. Portion of antenna.
Fig. 2. Section of antenna-wall, showing structure of *a a a* (fig. 1). Diameter $\frac{1}{1900}$ of an inch.
Fig. 3. Section of antenna-wall.
c c. Shows section of fig. 1 *c c*.
b b. Shows section of fig. 1 *b b*. } Diameter $\frac{1}{2800}$ of an inch.
d d. Shows section of fig. 1 *d d*. Diameter $\frac{1}{1300}$ of an inch.

P. *Antenna of* Sirex gigas.

Fig. 1. One segment, showing two kinds of organs:—
a. With elevated closing-in membrane (see P. fig. 4). Diameter $\frac{1}{3000}$ of an inch.
b. Cup-shaped membrane (see fig. 2 and fig. 3 *b*). Diameter $\frac{1}{900}$ of an inch.
Fig. 2. Section showing the cup-shaped organs.
Fig. 3. Superficial view.
Fig. 4. Section of antenna-wall through fig. 1 *a d*, fig. 3 *a*.

Q. *Antenna of* Arctia Caja.

Fig. 1. One segment of male antenna. The organs are chiefly on the extremity of the lateral pecten, scales being on the opposite aspect.
Fig. 2. Segments of female antenna. Organs on serrated aspect.
Fig. 3. Magnified apex of serræ, with organs. The dotted lines represent the interior condition.
Fig. 4. Apex of club-headed pecten of *Odonestis potatoria*.
a a. Organs. *b b*. Hairs.
Fig. 5. Enlarged view of an organ (*a*) and hair (*b*), with the cuticular lines.

R. *Antenna of* Tryphæna Bomba.

Fig. 1. External aspect of a segment. (All are alike.)
a. Scales on one side.
b b. Organs on opposite side, with small hairs between.
Fig. 2. Longitudinal section of ditto, showing nerve: *a* and *b*. lobulated matter beneath organs.
Fig. 3. Enlarged view of organs. *a a*. Organs. Between are hairs and cuticular markings.